



ENSO Drove 2500-Year Collapse of Eastern Pacific Coral Reefs

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to have been enhanced by its timing and location, allowing the Asian monsoon anticyclone to enhance the vertical transport while confining the majority of the aerosol to Asia and the Middle East until August, rather than rapidly mixing zonally and spreading throughout both hemispheres. The negative radiative forcing resulting from the 2011 Nabro eruption continues the trend from small eruptions of the past decade (13, 14), but the inherently variable nature of volcanic eruptions means that any short-term future cooling of the surface from volcanic stratospheric aerosol is uncertain.

References and Notes

1. P. Hamill, E. J. Jensen, P. B. Russell, J. J. Bauman, *Bull. Am. Meteorol. Soc.* **78**, 1395 (1997).
2. Global Volcanism Program, Smithsonian Institution; <http://www.volcano.si.edu/world/volcano.cfm?vnum=0201-101&volpage=weekly>.
3. NASA Laboratory for Atmospheres, Science Highlights, July 2011; available at <http://atmospheres.gsfc.nasa.gov/science/slides.php?sciid=9>.
4. E. J. Llewellyn *et al.*, *Can. J. Phys.* **82**, 411 (2004).
5. W. J. Randel *et al.*, *Science* **328**, 611 (2010).
6. D. Hofmann, J. Barnes, M. O'Neill, M. Trudeau, R. Neely, *Geophys. Res. Lett.* **36**, L15808 (2009).
7. J.-P. Vernier, L. W. Thomason, J. Kar, *Geophys. Res. Lett.* **38**, L07804 (2011).
8. G. K. Yue, M. P. McCormick, E. W. Chiu, *J. Geophys. Res.* **96**, (D3), 5209 (1991).
9. M. P. McCormick, R. E. Veiga, *Geophys. Res. Lett.* **19**, 155 (1992).
10. M. P. McCormick, L. W. Thomason, C. R. Trepte, *Nature* **373**, 399 (1995).
11. E. G. Dutton, J. R. Christy, *Geophys. Res. Lett.* **19**, 2313 (1992).
12. A. Robock, *Rev. Geophys.* **38**, 191 (2000).
13. J.-P. Vernier *et al.*, *Geophys. Res. Lett.* **38**, L12807 (2011).
14. S. Solomon *et al.*, *Science* **333**, 866 (2011).
15. D. Murtagh *et al.*, *Can. J. Phys.* **80**, 309 (2002).
16. A. E. Bourassa, D. A. Degenstein, E. J. Llewellyn, *J. Quant. Spectrosc. Radiat. Transf.* **109**, 52 (2008).
17. A. E. Bourassa, D. A. Degenstein, R. L. Gattinger, E. J. Llewellyn, *J. Geophys. Res.* **112**, D10217 (2007).
18. A. E. Bourassa, L. A. Rieger, N. D. Lloyd, D. A. Degenstein, *Atmos. Chem. Phys.* **12**, 605 (2012).
19. S. Fueglistaler *et al.*, *Rev. Geophys.* **47**, RG1004 (2009).
20. B. Kravitz, A. Robock, A. E. Bourassa, *J. Geophys. Res.* **115**, D00L05 (2010).
21. A. E. Bourassa, D. A. Degenstein, B. J. Elash, E. J. Llewellyn, *J. Geophys. Res.* **115**, D00L03 (2010).
22. J. M. Haywood *et al.*, *J. Geophys. Res.* **115**, D21212 (2010).
23. A. J. Prata, S. A. Carn, A. Stohl, J. Kerkmann, *Atmos. Chem. Phys.* **7**, 5093 (2007).
24. C. R. Trepte, M. H. Hitchman, *Nature* **355**, 626 (1992).
25. R. A. Plumb, *J. Geophys. Res.* **101**, 3957 (1996).
26. M. Park, W. J. Randel, A. Gettelman, S. T. Massie, J. H. Jiang, *J. Geophys. Res.* **112**, D16309 (2007).
27. T. Deshler, M. E. Hervig, D. J. Hofmann, J. M. Rosen, J. B. Liley, *J. Geophys. Res.* **108**, 4167 (2003).

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Supplementary Materials

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Figs. S1 to S4

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ENSO Drove 2500-Year Collapse of Eastern Pacific Coral Reefs

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Cores of coral reef frameworks along an upwelling gradient in Panamá show that reef ecosystems in the tropical eastern Pacific collapsed for 2500 years, representing as much as 40% of their history, beginning about 4000 years ago. The principal cause of this millennial-scale hiatus in reef growth was increased variability of the El Niño–Southern Oscillation (ENSO) and its coupling with the Intertropical Convergence Zone. The hiatus was a Pacific-wide phenomenon with an underlying climatology similar to probable scenarios for the next century. Global climate change is probably driving eastern Pacific reefs toward another regional collapse.

Global climate change is altering coral reef ecosystems through increasing sea temperatures and declining carbonate saturation states (1, 2). Warmer and more acidic conditions inhibit coral calcification, carbonate precipitation, and submarine cementation (3–5). These effects are expected to reduce long-term rates of reef framework construction. Here we provide an explicit test of this prediction by showing how vertical reef accretion in the tropical eastern Pacific (TEP) responded to climatic oscillations during the Holocene. Increased variability of the El Niño–Southern Oscillation (ENSO) ~4000 years ago produced conditions in the TEP similar to those expected under plausible scenarios of future climate, stalling reef

accretion off the Pacific coast of Panamá for 2500 years.

Living coral assemblages in the TEP respond to two principal environmental drivers: upwelling on a seasonal scale (6) and ENSO on a multiannual scale (7). The depressed water temperatures and reduced pH levels that accompany seasonal upwelling reduce coral growth (6). High sea temperatures associated with El Niño events cause bleaching, which reduces coral growth or kills corals outright (7). Mass coral mortality has been followed by intense bioerosion and the net loss of reef framework on a multidecadal scale (8). Upwelling and El Niño events are thought to account for generally poor Holocene reef development in the TEP (6, 7, 9), but neither has

been explicitly linked to millennial-scale rates of reef accretion. We investigated the history of reef framework construction along an upwelling gradient in Pacific Panamá and evaluated the influences of seasonal upwelling and ENSO on the tempo and mode of reef development.

The uncemented reef frameworks of the TEP consist of coral fragments packed in fine sediment. We extracted 14 push-cores from subtidal reef-slope habitats on three reefs across Pacific Panamá with distinct upwelling regimes (10). Isla Contadora, in the Gulf of Panamá, experiences intense seasonal upwelling; upwelling is intermediate at Isla Iguana, also in the Gulf of Panamá; and there is no upwelling at Isla Canales de Tierra in the Gulf of Chiriquí

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(Fig. 1). This upwelling gradient was established at least as early as the mid-Holocene (11) (table S1).

Each core was extruded and sectioned into 5-cm intervals. The coral constituents of the intervals were sorted by species and taphonomic condition to identify layers representing different modes of reef development. Layers were dated with three methods: ^{14}C analysis by standard techniques and accelerator mass spectrometry (AMS), and U/Th analysis by inductively coupled plasma mass spectrometry (ICP-MS). Radiocarbon dates were calibrated using the marine calibration curve and the local reservoir correction (fig. S1 and tables S1 and S2). Accretion rates were calculated by dividing the depth range of each interval in the framework by its time span (10).

The cores were dominated by well-preserved skeletons of *Pocillopora damicornis* (Fig. 2A), which is the primary constructor of modern reef framework in the TEP. A sample of well-preserved *Pocillopora*, resting directly atop the basaltic bedrock in one core, indicated that reef growth had begun by 6900 calibrated calendar

years before the present (cal yr B.P.) (where the present is 1950). Each core contained a narrow interval dominated by a combination of taphonomically degraded *Pocillopora* rubble, branching coralline algae, and *Psammocora stellata*, which does not build framework. This narrow interval represents a millennial-scale hiatus in active reef development, from 4220 to 4064, until 1820 to 1520 cal yr B.P.

Despite concentrated dating of corals within and around the interval of limited deposition in the cores (25 standard, 16 AMS, and 19 ICP-MS dates), no samples of *Pocillopora* dated within the interval 4064 to 1820 cal yr B.P. Dated samples of *Psammocora* in the hiatus (12 AMS and 5 ICP-MS dates) indicated that this coral stopped growing by 4332 cal yr B.P. (2σ range: 4442 to 4186). *Psammocora* recovered by 2384 cal yr B.P. at the earliest (2σ range: 2522 to 2289); thus, coral growth restarted several centuries before framework accretion resumed.

Accretion rates were significantly reduced at all sites during the hiatus as compared with intervals of active reef growth before and after [Fig. 2B and table S3; analysis of variance

(ANOVA), $F_{2,29} = 64.001$, $P < 0.001$, Tukey's honestly significant difference (HSD) $P < 0.001$]. During active reef growth, average rates of vertical accretion were similar among our sites and were comparable to rates for Caribbean reefs (table S4). The slower overall accretion rates in the Gulf of Panamá reported previously (9) resulted from differences in the timing of the hiatus among environments. The hiatus began at approximately the same time at all sites (ANOVA $F_{2,9} = 2.276$, $P = 0.158$; table S5); however, it ended later and lasted longer at Contadora, the strong-upwelling site, as compared with Canales de Tierra, where there was no upwelling (ANOVA, $F_{2,9} = 8.390$, $P = 0.009$; $F_{2,9} = 6.189$, $P = 0.020$; Tukey HSD, $P < 0.05$, tables S6 and S7). No significant differences were found in the timing of the hiatus between either site and Iguana (Tukey HSD, $P > 0.05$).

Contemporaneous millennial-scale hiatuses in reef development have been recorded in Golfo Dulce, Costa Rica (12), and in inshore sections of the Great Barrier Reef and Moreton Bay, Australia (table S8) (13, 14). Likewise, an intermittent hiatus in Japan coincided with the onset of the hiatus in Pacific Panamá (15). These events, previously attributed to local- or regional-scale phenomena, are more likely the result of Pacific-wide climatic changes that disrupted reef development in the nearshore environments of many regions simultaneously.

The hiatus corresponds to a time of enhanced climatic variability (Fig. 3). ENSO frequency and intensity increased beginning 4500 to 4000 cal yr B.P. (16–20), coincident with the onset of the hiatus in our cores. A concurrent period of high variability in the latitudinal migration of the Intertropical Convergence Zone (ITCZ) (Fig. 3B) suggests that the coupled influence of ENSO and the ITCZ caused the increase in ENSO strength (16, 19); reconstructions suggest that El Niño events occurring 4000 to 2000 cal yr B.P. were among the strongest of the Holocene (18) (Fig. 3C).

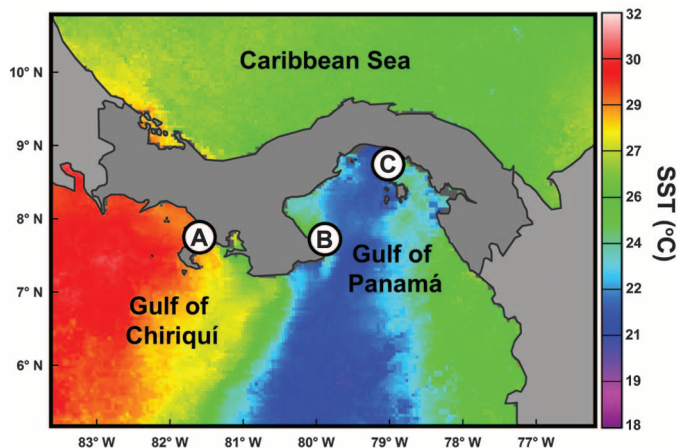
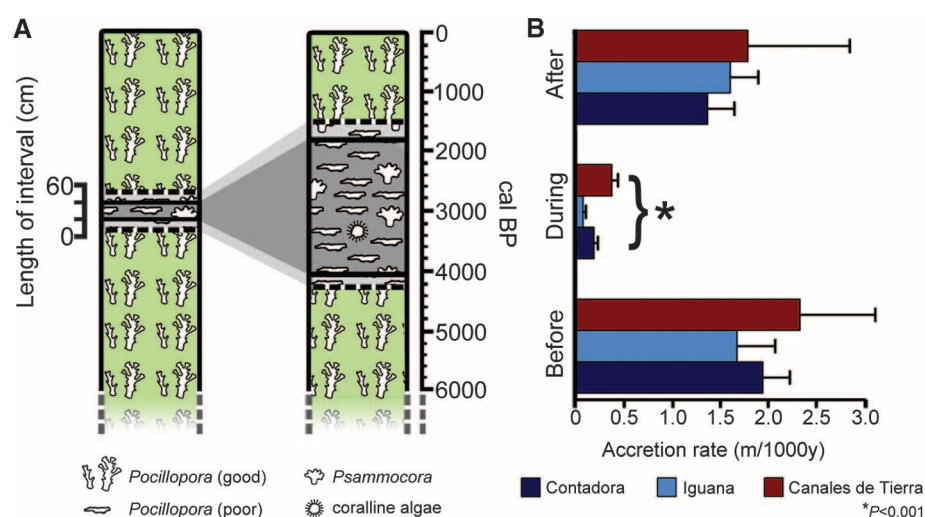


Fig. 1. Map of Pacific Panamá showing the locations of study reefs in relation to upwelling regimes. A, Canales de Tierra. B, Iguana. C, Contadora. The coloration shows sea-surface temperature (SST) at the peak of the 2009 upwelling season, 4 to 17 March. The image was created from MODIS/Aqua Satellite SST data using NASA's POET v.2.0 software (<http://poet.jpl.nasa.gov>).

Fig. 2. (A) Composite core log. Green shading with icons of *Pocillopora* in good taphonomic condition indicates periods of active reef growth. Gray shading with icons of *Pocillopora* in poor condition, *Psammocora*, and coralline algae indicates interrupted reef accretion. The length of the hiatus (gray shading) is shown expanded to depth in the reef framework (left) and in calibrated calendar years before the present (right). Dark gray shading represents the most conservative time span for the hiatus; light gray shading shows the maximum range based on all three sites. (B) Mean accretion rates before, during, and after the hiatus. Error bars represent standard errors; the asterisk indicates significant difference from the other groups ($P < 0.001$).



Very strong El Niño events beginning ~4200 cal yr B.P. (Fig. 3D) (16–18, 20, 21) could have caused the initial collapse of coral populations in Pacific Panamá because of bleaching-related mortality (7). ENSO activity peaked ~3000 cal yr B.P. (Fig. 3E), with stronger and more frequent El Niño events than at any other time during the Holocene (20–22). Frequent high-temperature anomalies would have precluded the recovery of coral populations, suppressing reef accretion.

More frequent La Niña events 3800 to 3200 cal yr B.P. (19) would also have inhibited reef development. Increased precipitation in Panamá during La Niña events (23) would have elevated turbidity and reduced light levels (14). On the high-turbidity reefs of the TEP (12), small changes in water clarity would likely have reduced light

levels below the threshold necessary for active development (24). Greater atmospheric pressure across the Pacific under La Niña conditions would have lowered sea levels in the TEP (25), subjecting corals more frequently to lethal sub-aerial exposure. Frequent thermal anomalies, reduced light fields, and repeated subaerial exposure all would have limited accretion rates during the hiatus.

ENSO activity continued to increase after the end of the hiatus (17, 19, 26); however, major changes in the mode of ENSO coincided with its termination (16, 18, 19). ENSO and the ITCZ decoupled ~2500 cal yr B.P. (19), accounting for the decline in variability of the ITCZ (16). There was also a reduction in La Niña activity ~2000 to 1500 cal yr B.P. (19, 27), which would have increased regional light availability and reduced

the frequency of subaerial exposure. Although the absolute number of El Niño events may have increased beginning 2000 cal yr B.P. (17, 19, 26, 27), the events were probably stronger during the hiatus (18). The waning influence of La Niña and reduction in El Niño strength apparently permitted active accretion to resume 1820 to 1520 cal yr B.P.

We propose that shifts in the frequency and intensity of ENSO, and especially its coupling with the ITCZ, were the ultimate cause of the depositional hiatus at our sites in Pacific Panamá and, perhaps, elsewhere in the Pacific (Fig. 4). Coral populations may have persisted on nearby reefs or in favorable microhabitats, facilitating the eventual recolonization of the reef slopes at Contadora, Iguana, and Canales de Tierra. Although climate change has been linked to reef development in deep time (28), sea-level changes have heretofore been considered the major control on reef development during the Quaternary (29). Our study, in contrast, implicates climatic oscillations as the primary driver of reef development during the Holocene. Reefs of the TEP are poorly developed, but not because coral growth was suppressed during their entire history by low sea temperatures and elevated partial pressure of CO₂ from upwelling, or by high sea temperatures from El Niño events with modern characteristics (3, 7). The reefs are poorly developed because coral populations collapsed for an interval spanning ~40% of their 6000- to 7000-year existence.

Alternative hypotheses fail to explain the duration, timing, or spatial extent of the hiatus. A sea-level highstand occurred in many parts of the Pacific ~6000 cal yr B.P. (13). Reduced light levels in Pacific Panamá could have drowned reefs at that time; however, there is no evidence of such a highstand in the TEP (30), and peak sea levels elsewhere occurred two millennia before the onset of the hiatus. The opposite scenario, in which the reefs filled the available accommodation space during the (putative) highstand and then stopped growing (13), cannot explain why vertical accretion abruptly resumed at a time when eustatic sea level was either still declining from the highstand or continuing a multimillennial rise (13, 31). Our sites were located well within the subtidal envelope from 6000 cal yr B.P. to the present (30), and there is no evidence of tectonic connections that would have allowed uplift or subsidence uniformly from the Gulf of Panamá to Golfo Dulce (32). The Pacific-wide distribution of the hiatus eliminates localized fluctuations of relative sea level or tectonics as the controlling influence.

Finally, extensive bioerosion of the subfossil framework by echinoids did not create an unconformity we detected as the hiatus. Although rates of bioerosion after ENSO-related disturbance can exceed rates of carbonate production (8), bioerosion does not cause significant information loss from the fossil record once the

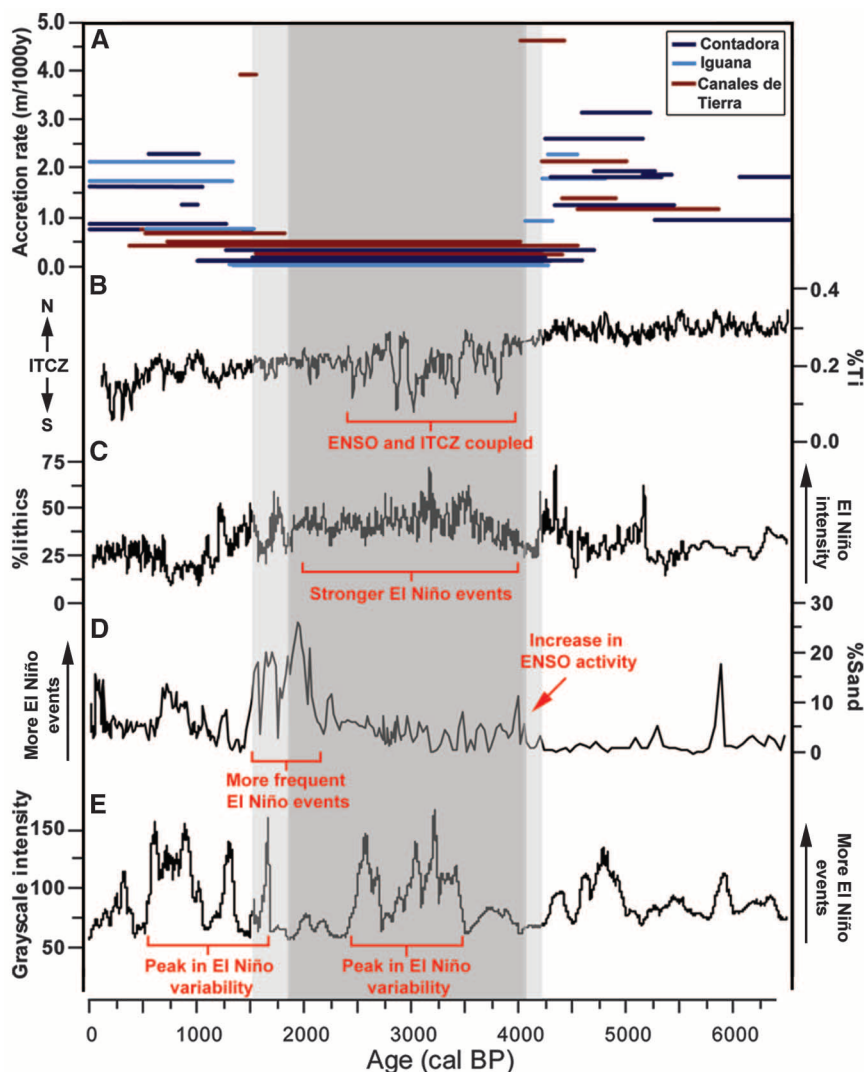


Fig. 3. Climatic reconstructions of ENSO-related precipitation as compared with accretion rates in the TEP. (A) Reef accretion, this study. (B) Percent of titanium in a deep-sea core from Cariaco Basin (16). (C) A 10-year running mean of the relative percent of lithic sediments in a deep-sea core off the coast of Peru (18). (D) Percent of sand in a core from El Junco Lake, San Cristobal, Galápagos (19). (E) A 50-year running mean of grayscale intensity in a core from Laguna Pallacocha, Ecuador (26). Gray shading is as in Fig. 2.

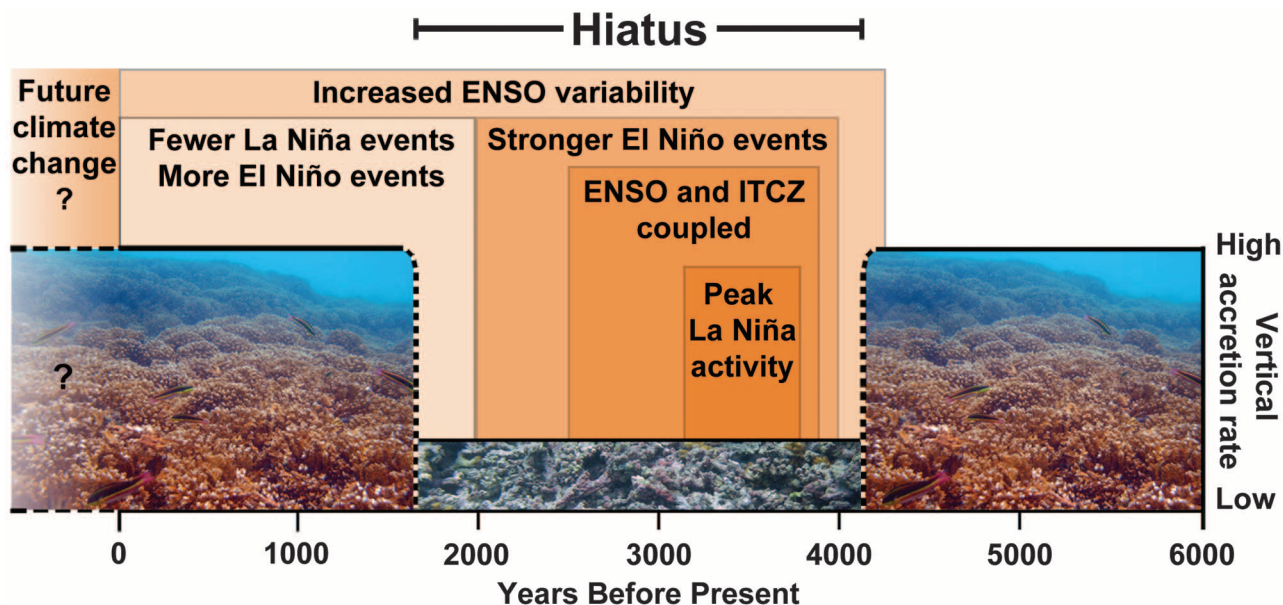


Fig. 4. Conceptual model of the climatic drivers of reef collapse in the TEP. Temporal ranges of climatic conditions are shown in orange, and community states are illustrated pictorially.

coral skeletons have been stabilized and packed in fine sediment. In our cores, the uppermost, open framework generally represented less than 100 years of depositional time. Bioerosion cannot explain the 2500-year hiatus, and the error due to bioerosion in estimating its timing is negligible. Furthermore, extensive bioerosion could be a modern phenomenon resulting from overfishing of the predators of echinoids (33).

Reef dynamics in the TEP and elsewhere in the Pacific have been driven by long-term shifts in ENSO variability for at least the past 6000 years. The intensity of seasonal upwelling acted as a second-order process, potentially influencing local ecosystem resilience. Ecological processes, including herbivory, corallivory, and competition, exerted imperceptible third-order effects on long-term rates of reef accretion, although biological interactions in refuges could have influenced the recovery of coral populations. The widespread distribution of the hiatus suggests that climatic variability was a controlling influence on reef accretion over a broad longitudinal range in the Pacific during the Holocene.

In recent years, ENSO activity has devastated tropical reefs (34). Enhanced ENSO-like conditions in a warming world (25) could once again put Pacific reefs at risk of collapse. The TEP is a low-diversity system in which a modern history of intense disturbance has driven acclimation and adaptation in the coral populations. Higher-diversity reef systems in the western Pacific that have experienced a relatively benign history of disturbance could be even more vulnerable to climate change (35). But if Pacific reefs were able to recover after a millennial-scale hiatus in coral growth, and if current trends in CO₂ emis-

sions can be stopped or reversed, reefs of the future might also prove resilient.

References and Notes

- O. Hoegh-Guldberg *et al.*, *Science* **318**, 1737 (2007).
- J. M. Pandolfi, S. R. Connolly, D. J. Marshall, A. L. Cohen, *Science* **333**, 418 (2011).
- D. P. Manzello *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 10450 (2008).
- G. De'ath, J. M. Lough, K. E. Fabricius, *Science* **323**, 116 (2009).
- N. E. Cantin, A. L. Cohen, K. B. Karnauskas, A. M. Tarrant, D. C. McCorkle, *Science* **329**, 322 (2010).
- P. W. Glynn, *J. Mar. Res.* **35**, 567 (1977).
- P. W. Glynn, M. W. Colgan, *Am. Zool.* **32**, 707 (1992).
- C. M. Eakin, *Coral Reefs* **15**, 109 (1996).
- P. W. Glynn, I. G. Macintyre, *Proc. 3rd Int. Coral Reef Symp.*, 251 (1992).
- Materials and methods are available as supplementary materials on Science Online.
- I. Martínez, D. Rincon, Y. Yokoyama, T. Barrows, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **234**, 114 (2006).
- J. Cortés, I. G. Macintyre, P. W. Glynn, *Coral Reefs* **13**, 65 (1994).
- C. T. Perry, S. G. Smithers, *Geology* **38**, 119 (2010).
- M. Lybolt *et al.*, *Front. Ecol. Environ.* **9**, 154 (2011).
- N. Hamanaka *et al.*, *Global Planet. Change* **80**, 21 (2012).
- G. H. Haug, K. A. Hughen, D. M. Sigman, L. C. Peterson, U. Röhl, *Science* **293**, 1304 (2001).
- M. A. Riedinger, M. Steinitz-Kannan, W. M. Last, M. Brenner, *J. Paleolimnol.* **27**, 1 (2002).
- B. Rein, *Quat. Int.* **161**, 56 (2007).
- J. L. Conroy, J. T. Overpeck, J. E. Cole, T. M. Shanahan, M. Steinitz-Kannan, *Quat. Sci. Rev.* **27**, 1166 (2008).
- T. H. Donders, F. Wagner-Cremer, H. Visscher, *Quat. Sci. Rev.* **27**, 571 (2008).
- T. Corrège *et al.*, *Paleoceanography* **15**, 465 (2000).
- M. K. Gagan, E. J. Hendy, S. G. Haberle, W. S. Hantoro, *Quat. Int.* **118–119**, 127 (2004).
- M. S. Lachniet *et al.*, *J. Geophys. Res.* **109**, D20117 (2004).
- J. A. Kleypas, *Paleoceanography* **12**, 533 (1997).
- M. Collins *et al.*, *Nat. Geosci.* **3**, 391 (2010).
- C. M. Moy, G. O. Seltzer, D. T. Rodbell, D. M. Anderson, *Nature* **420**, 162 (2002).
- H. Yan *et al.*, *Nat. Geosci.* **4**, 611 (2011).
- R. Wood, *Reef Evolution* (Oxford Univ. Press, New York, 1999).
- R. W. Buddemeier, D. Hopley, *Proc. 6th Int. Coral Reef Symp.*, 253 (1988).
- J. R. Curray, F. J. Emmel, P. J. S. Crampton, *Lagunas Costeras, Un Simposio, Memorias del Simposio Internacional sobre Lagunas Costeras*, A. A. Castañares, F. B. Phleger, Eds. (Universidad Nacional Autónoma de México—United Nations Educational, Scientific, and Cultural Organization, México, D.F., 1969), pp. 63–100.
- M. A. Toscano, I. G. Macintyre, *Coral Reefs* **22**, 257 (2003).
- U.S. Geological Survey, *U.S. Geol. Surv. Open-File Rep.* 98-779 (1998).
- J. L. Sonnenholzner, L. B. Ladah, K. D. Lafferty, *Mar. Ecol. Prog. Ser.* **375**, 209 (2009).
- A. C. Baker, P. W. Glynn, B. Riegl, *Estuar. Coast. Shelf Sci.* **80**, 435 (2008).
- D. M. Thompson, R. van Woesik, *Proc. Biol. Sci.* **276**, 2893 (2009).

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Supplementary Materials

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Fig. S1
Tables S1 to S8
References (36–57)

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Supplementary Materials for

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Materials and Methods

Coring and core-processing methodologies

We extracted a total of 14 push-cores from reef frameworks at Contadora ($N=5$), Iguana ($N=4$), and Canales de Tierra ($N=5$). The cores were collected at each site from the fore-reef slope, where reef accretion is most rapid (9). Small-scale interruptions of reef development are more frequent in more marginal reef zones (i.e., the reef flat and back reef), whereas only larger-scale interruptions in reef development are likely to be observed in the subfossil record of the reef slope; therefore, this zone was the ideal environment to detect regional-scale hiatuses in reef development. For each core, divers forced a 5- to 6-m length of 7.6-cm (3-in) diameter aluminum tubing into the reef using adjustable core slips with handles. A sliding hammer-weight, sleeved over the top of the tube, facilitated penetration. Recovery was measured periodically during the coring operation by dropping a weighted surveyor's tape down the open tube and subtracting the depth of the top of the material within the tube from the total length of the tube. Penetration was calculated by measuring the length of the tube protruding from the reef surface and subtracting from the total length. Compaction was calculated as recovery divided by penetration. When all but 1 m of the core tube had been driven into the reef framework, the core was capped, pulled from the reef using the core handles, and sealed. A detailed description of the coring methodology may be found elsewhere (36, 37).

The cores were extruded in the laboratory, and the cored material was divided into 5-cm sections. Each 5-cm section was sieved and cleaned. Core constituents >2 mm in longest dimension, almost all of which were fragments of *Pocillopora* spp. and *Psammocora stellata*, were sorted by species and taphonomic condition. Categorical grades of taphonomic condition were assigned based on the degree of encrustation, erosion, and superficial boring of the coral fragment. If the total alteration of the surface was $<20\%$ of the surface area, the corals were considered to be in good condition; 20–50% alteration was categorized as intermediate condition, and $>50\%$ alteration was categorized as poor condition. Coralline algae, shells, and unclassified rubble were also separated. The sorted core constituents were weighed and their masses were compared among intervals.

Intervals indicative of active reef development in the cores were dominated by *Pocillopora* spp. in good to intermediate condition. Periods of interrupted reef development—the hiatus and other, short-term interruptions—were characterized by intervals in the cores dominated by coralline algae, *Pocillopora* in poor condition, or *Psammocora stellata*. Dating of layers of active and interrupted reef development revealed the timing of initiation and termination of the hiatus for each core at each site, as well as rates of vertical reef accretion through time (discussed below).

Radiocarbon reservoir correction for Pacific Panamá

Radiocarbon dating of corals is influenced by the ages of regional water masses (reservoir ages); therefore, ^{14}C ages of corals must be calibrated using local reservoir corrections (38, 39). Typically, a global reservoir correction is applied using the standard marine calibration curve (39, 40); however, upwelling introduces old carbon into the surface waters. The offsets between the true ages of carbonates and the reservoir ages are, therefore, especially pronounced in upwelling regions (e.g. Pacific Panamá; 40–44).

Where the local reservoir age deviates significantly from the global reservoir correction, independent calibration of ^{14}C ages is necessary to determine ΔR , the deviation from the standard reservoir correction (39). If $\Delta\text{R}\neq 0$, it is incorporated into the calibration of measured radiocarbon dates.

U/Th dating is not subject to reservoir effects and provides an independent proxy for the true age of marine carbonates (45, 46). The difference between the radiocarbon age and the U/Th age of a carbonate sample gives an estimate of the local reservoir correction at a given time (47). Temporal fluctuations in the reservoir age can be indicative of changes in the intensity of regional upwelling (42, 43, 48).

Individual fragments of subfossil coral skeleton, located below or above the hiatus in our cores at Contadora ($N=7$), Iguana ($N=4$), and Canales de Tierra ($N=4$) Islands, were split: one half was radiocarbon-dated using AMS and the other half was dated with U/Th using ICP-MS. Blind samples were measured by Beta Analytic, Inc. and H. Cheng, respectively. The differences between the U/Th and radiocarbon ages of the corals were used to determine R , the reservoir age. The difference between the measured ^{14}C age and the intercept of the marine calibration curve, minus the corresponding U/Th age, gives ΔR (Table S1).

The means of ΔR for Contadora and Iguana were within one standard deviation (mean $\Delta\text{R}=169.8\pm 162.8$ and $\Delta\text{R}=192.8\pm 150.1$, respectively). At Canales de Tierra, ΔR was zero for all four coral samples, reflecting the negligible influence of upwelling in the Gulf of Chiriquí (Table S1). There were large differences in ΔR before and after the hiatus at Contadora and Iguana (mean $\Delta\text{R}_{\text{before}}=278.0\pm 94.07$ and $\Delta\text{R}_{\text{after}}=60.1\pm 33.2$; Figure S1).

The differences in ΔR between sites (Contadora and Iguana) and periods (before and after the hiatus) were analyzed statistically with a two-way ANOVA. Because the reservoir correction at Canales de Tierra did not deviate from the global reservoir correction, data from this site were not included in the analysis. The raw ΔR data conformed to the assumptions of homoscedasticity (Levene's test: $F_{3,7}=2.185$, $P=0.178$) and normality (Shapiro-Wilk test: $W_{11}=0.951$, $P=0.652$), so no transformation of the data was necessary. ΔR was significantly higher before the hiatus ($F_{1,7}=25.091$, $P=0.002$; Fig. S1; Table S2). The differences between Contadora and Iguana and the interaction between site and period were non-significant ($F_{1,7}<0.001$, $P=0.996$; $F_{1,7}=1.013$, $P=0.348$, respectively).

ΔR was zero for Canales de Tierra, so the calibrated radiocarbon dates obtained using standard marine calibration are accurate. For Contadora and Iguana, values of ΔR were incorporated into the calibration of measured radiocarbon dates. Because there was no significant difference in ΔR between Contadora and Iguana, we used the ΔR value that was closest to the ^{14}C age of the sample, regardless of the site from which it came.

Statistical analysis

Vertical accretion rates were compared among sites (Contadora, Iguana, and Canales de Tierra) and periods (before, during, and after the hiatus) with a two-way analysis of variance (ANOVA), using a general linear model to account for unequal sample sizes (Table S3). The raw data failed to meet the assumption of homoscedasticity (Levene's test: $F_{8,29}=4.356$, $P=0.002$); therefore, the data were natural-log transformed. After

transformation, the data conformed to the assumptions of homoscedasticity (Levene's test: $F_{8,29}=1.661$, $P=0.151$) and normality (Shapiro–Wilk test: $W_{38}=0.969$, $P=0.372$).

The dates for the initiation, duration, and termination of the hiatus were compared among sites with one-way ANOVAs using general linear models (Tables S5–S7). The raw data for initiation and termination of the hiatus conformed to the assumptions of homoscedasticity (Levene's test: $F_{2,9}=3.210$, $P=0.089$; $F_{2,9}=1.861$, $P=0.211$, respectively) and normality (Shapiro–Wilk test: $W_{12}=0.933$, $P=0.410$; $W_{12}=0.905$, $P=0.184$, respectively); therefore, no transformation of the data was necessary. The duration data were heteroscedastic (Levene's test: $F_{2,9}=1.100$, $P=0.374$), but non-normal (Shapiro–Wilk test: $W_{12}=0.843$, $P=0.030$). The data were rank-transformed, equating the parametric ANOVA to the non-parametric Kruskal–Wallis test and eliminating the requirements of homoscedasticity and normality (49).

Reef accretion compared to other localities

Recoveries measured from the extruded cores were generally equal to, or nearly equal to, the corresponding final recoveries measured in the field prior to extraction. The extruded cores, which had been compacted during the coring process, were re-expanded in segments, using the *in situ* measurements of compaction. To calculate rates of vertical reef accretion in intervals of active and interrupted reef growth, we divided the expanded length of an interval by the time over which that interval had accreted.

Accretion rates in Pacific Panamá before and after the hiatus were averaged. These values from outside the hiatus were compared to average bulk (whole-core) accretion rates from other localities (Table S4). In order to make direct comparisons between localities, we only included studies that met four criteria. First, the cores were collected from the outer slopes of reefs exposed to moderate wave energy, like those in the present study. Second, the reefs were constructed of branching-coral frameworks, typically *Acropora* spp. in both the Caribbean and western Pacific, and *Pocillopora* spp. in the tropical eastern Pacific (TEP). Third, accretion rates were calculated with calibrated radiocarbon dates; alternatively, data on core penetrations and un-calibrated ages were provided, permitting calibration and recalculation of accretion rates. Fourth, the dates used in the calculations were at least 1000 cal BP, because more recent accretion rates can be inflated by instantaneous coral-growth rates and a lack of compaction.

Radiocarbon dates from Punta Islotes, Costa Rica (12), Galeta Point, Panamá (50), Bahía Almirante, Panamá (51), and the central shelf lagoon in Belize (37) were reported as uncalibrated ^{14}C ages. These dates were calibrated using Calib 5.0 (52, 53), and the accretion rates were recalculated. A coring study in Jamaica (54) included only one radiocarbon date greater than 1000 cal BP, so we estimated reef accretion from a single core and report it without associated error. The site at Punta Islotes, Costa Rica (12) exhibits a hiatus that is contemporaneous with the hiatus reported in this paper; therefore, average post-hiatus accretion is reported from Punta Islotes. Finally, ranges of average bulk-accretion rates of reefs across the Indo-Pacific are compiled from Montaggioni's (55) review of Pacific reef development during the Holocene.

Coral reefs in the TEP are generally thought to be poorly-developed compared to other regions (56); however, rates of framework accretion in Pacific Panamá during periods of active reef growth are comparable to bulk accretion rates in the Caribbean,

with few exceptions (e.g., 57). Accretion rates are higher in many parts of the Indo-west Pacific compared to Pacific Panamá, but there are a number of locations where reef accretion is similar to our sites. Average vertical accretion was more rapid in Costa Rica compared to our sites, but the difference is within the range of error.

Concurrent hiatuses in the Pacific

The 2500-year hiatus in Pacific Panamá was contemporaneous with millennial-scale interruptions in reef development elsewhere in the Pacific (Table S8). These other hiatuses were identified from published reports, in which intervals of active and interrupted reef development were identified using radiocarbon dating. Hiatuses were characterized by temporal gaps in the records of coral deposition. Uncalibrated radiocarbon dates from the reef at Punta Islotes, Golfo Dulce, Costa Rica (12), were calibrated using Calib 5.0, as discussed above. Dates from Moreton Bay, Cockermouth reef, and Cape Tribulation, all in Australia, as well as the reef at Kodakara Island in Japan, were reported in cal BP (12–15), so no further calibration was necessary. Lybolt et al. (14) suggested that the hiatus in Moreton Bay, Australia lasted from 4150–800 cal BP; however, two corals in their study dated to ~2000 cal BP, so we used this date as a conservative endpoint for that hiatus. For simplicity, we combined data from Low Isles reef with that of reefs at Cape Tribulation, Australia (13), although the former site is located offshore from Cape Tribulation proper. We report data from a single reef in the southern Great Barrier Reef, Cockermouth, because the stratigraphy at this site is the most complete for the region (13). The hiatus in Japan was intermittent (15), but its initiation corresponds to the collapse of reef communities in Pacific Panamá.

Permits

Fieldwork was carried out under permits from the Autoridad Marítima de Panamá, the Autoridad Nacional del Ambiente de Panamá, and the Dirección Nacional de Recursos Minerales and Autoridad de los Recursos Acuáticos de Panamá. Export permits were obtained from the Dirección Nacional de Aduanas.

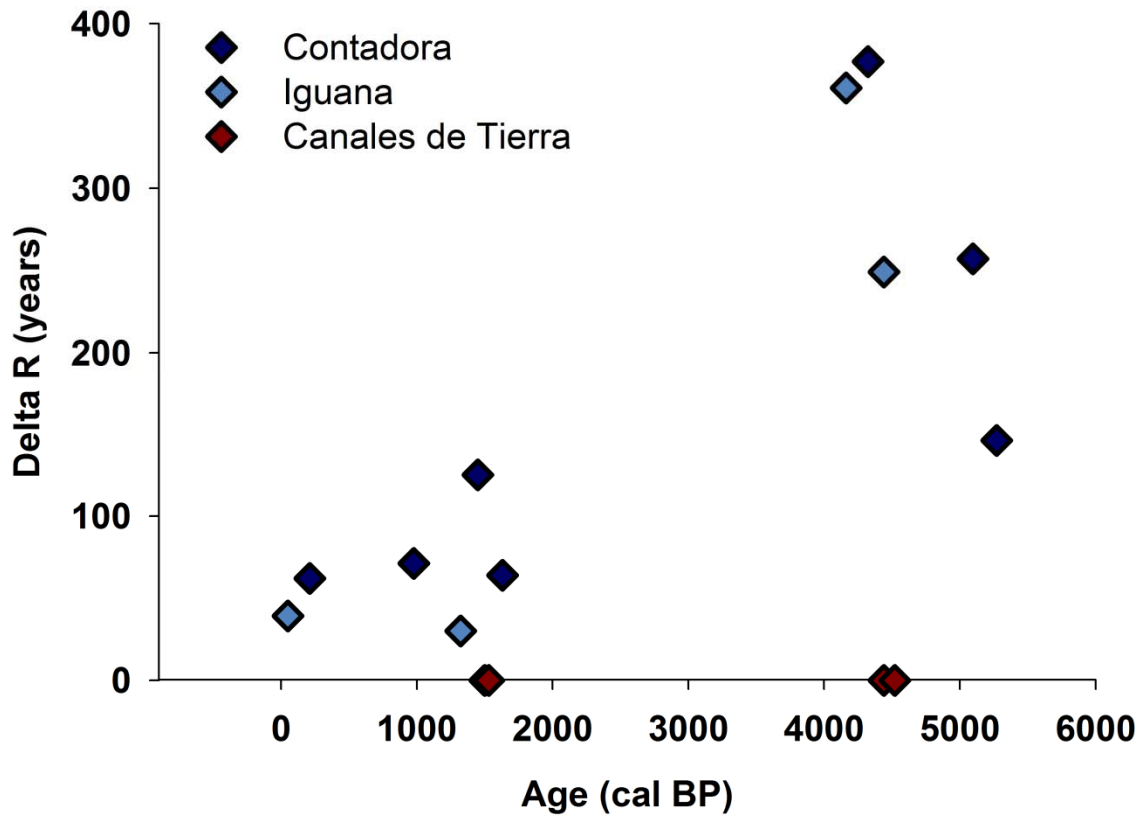


Figure S1. ΔR values over time at Contadora, Iguana, and Canales de Tierra.

Table S1. Uncalibrated, “conventional” ^{14}C ages and calibrated U/Th ages of coral samples from Contadora, Iguana, and Canales de Tierra. R is the difference between these ages. ΔR is calculated using the measured ages and the marine calibration curve (Cal- ^{14}C). ^{14}C and Cal- ^{14}C ages are reported in years before 1950 (yr BP and cal BP). U/Th ages are given in cal BP. R and ΔR are reported in years. All errors are reported as 2 standard deviations.

Location	Core ID	Coral genus	^{14}C age	U/Th age	R	Cal- ^{14}C	ΔR
Contadora	EP08-25	<i>Pocillopora</i>	600±25	212±7	388	538±25	62
	EP08-25	<i>Pocillopora</i>	1520±80	978±12	542	1449±25	71
	EP08-26	<i>Pocillopora</i>	5060±30	5271±20	-211	4914±26	146
	EP09-27	<i>Psammocora</i>	2030±80	1450±8	580	1905±26	125
	EP09-27	<i>Psammocora</i>	2130±80	1630±22	500	2066±27	64
	EP09-27	<i>Pocillopora</i>	4590±80	4322±19	268	4213±26	377
	EP09-28	<i>Pocillopora</i>	5080±40	5096±27	-16	4823±26	257
Iguana	EP07-15	<i>Pocillopora</i>	1820±80	1323±16	497	1790±26	30
	EP07-16	<i>Pocillopora</i>	495±25	52±14	443	456±23	39
	EP07-16	<i>Pocillopora</i>	4480±80	4162±101	318	4119±26	361
	EP07-16	<i>Pocillopora</i>	4580±80	4440±12	140	4330±26	249
Canales de Tierra	EP10-34	<i>Pocillopora</i>	1940±30	1500±32	440	1940±27	0
	EP10-34	<i>Pocillopora</i>	4330±30	4440±32	-110	4330±26	0
	EP10-35	<i>Pocillopora</i>	1980±30	1530±32	450	1980±27	0
	EP10-35	<i>Pocillopora</i>	4380±30	4520±32	-140	4380±25	0

Table S2. Two-way ANOVA comparing ΔR values between Contadora and Iguana and before and after the hiatus.

Source	SS	df	MS	<i>F</i>	<i>P</i>
Period	1.283×10^5	1	1.283×10^5	25.091	0.002
Site	0.158	1	0.158	<0.001	0.996
Period x Site	5.173×10^3	1	5.173×10^3	1.013	0.348
Error	3.576×10^4	7	5.109×10^3		
Total	4.526×10^5	11			

Table S3. Two-way ANOVA comparing square-root-transformed accretion rates among periods and sites.

Source	SS	df	MS	<i>F</i>	<i>P</i>
Period	25.958	2	12.979	64.001	<0.001
Site	0.739	2	0.369	1.821	0.180
Period x Site	1.279	4	0.320	1.576	0.207
Error	5.881	29	0.203		
Total	34.550	38			

Table S4. Average bulk-accretion rates (\pm SD) during the Holocene in the TEP outside the hiatus compared to the Caribbean. Ranges of accretion rates in other parts of the Pacific and the Indian Oceans are also reported. The ranges for each region are derived from averages within sites. All rates are reported in meters per 1000 years. Sample size (N) refers to the number of cores.

Location	Accretion rate	N	Reference
Tropical Eastern Pacific			
<i>Isla Contadora, Panamá</i>	1.60 \pm 0.69	5	this study
<i>Isla Iguana, Panamá</i>	1.82 \pm 0.70	3	this study
<i>Isla Canales de Tierra, Panamá</i>	2.38 \pm 0.97	2	this study
<i>Punta Islotes, Costa Rica</i>	2.42 \pm 0.23	3	(12)
Caribbean			
<i>Bahía Almirante, Panamá</i>	1.48 \pm 0.45	33	(51)
<i>Galeta Point, Panamá</i>	1.52 \pm 0.31	6	(50)
<i>Central shelf lagoon, Belize</i>	2.05 \pm 0.86	8	(37)
<i>Discovery Bay, Jamaica</i>	2.48	1	(54)
Central Pacific			
<i>Society Islands</i>	10–36		(55) and references therein
Western Pacific			
<i>Great Barrier Reef</i>	3.5–10.3		
<i>Other localities</i>	1.2–7.7		
Indian Ocean			
<i>Eastern Indian Ocean</i>	7–25		
<i>Western Indian Ocean</i>	0.8–3		

Table S5. One-way ANOVA comparing the timing of initiation of the hiatus among sites.

Source	SS	df	MS	<i>F</i>	<i>P</i>
Site	1.094×10^5	2	5.472×10^4	2.276	0.158
Error	2.164×10^5	9	2.404×10^4		
Total	2.267×10^8	12			

Table S6. One-way ANOVA comparing the timing of termination of the hiatus among sites.

Source	SS	df	MS	<i>F</i>	<i>P</i>
Site	5.065×10^5	2	2.532×10^5	8.390	0.009
Error	2.717×10^5	9	3.018×10^4		
Total	2.324×10^7	12			

Table S7. One-way ANOVA comparing the rank of duration of the hiatus among sites.

Source	SS	df	MS	<i>F</i>	<i>P</i>
Site	82.800	2	41.400	6.189	0.020
Error	60.200	9	6.689		
Total	650.000	12			

Table S8. Location and timing of concurrent hiatuses in the Pacific.

Location	Site	Hiatus (Cal BP)	Reference
Pacific Panamá	Contadora	4252–1520	this study
	Iguana	4064–1553	this study
	Canales de Tierra	4220–1820	this study
Costa Rica	Golfo Dulce	4618–2048	(12)
Great Barrier Reef	Moreton Bay	4150–2000	(14)
	Cockermouth	5426–2605	(13)
	Cape Tribulation	4074–2330	(13)
Japan	Kodakara Island	4400–3200	(15)

References and Notes

1. O. Hoegh-Guldberg *et al.*, Coral reefs under rapid climate change and ocean acidification. *Science* **318**, 1737 (2007). [doi:10.1126/science.1152509](https://doi.org/10.1126/science.1152509) [Medline](#)
2. J. M. Pandolfi, S. R. Connolly, D. J. Marshall, A. L. Cohen, Projecting coral reef futures under global warming and ocean acidification. *Science* **333**, 418 (2011). [doi:10.1126/science.1204794](https://doi.org/10.1126/science.1204794) [Medline](#)
3. D. P. Manzello *et al.*, Poorly cemented coral reefs of the eastern tropical Pacific: Possible insights into reef development in a high-CO₂ world. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 10450 (2008). [doi:10.1073/pnas.0712167105](https://doi.org/10.1073/pnas.0712167105) [Medline](#)
4. G. De'ath, J. M. Lough, K. E. Fabricius, Declining coral calcification on the Great Barrier Reef. *Science* **323**, 116 (2009). [doi:10.1126/science.1165283](https://doi.org/10.1126/science.1165283)
5. N. E. Cantin, A. L. Cohen, K. B. Karnauskas, A. M. Tarrant, D. C. McCorkle, Ocean warming slows coral growth in the central Red Sea. *Science* **329**, 322 (2010). [doi:10.1126/science.1190182](https://doi.org/10.1126/science.1190182) [Medline](#)
6. P. W. Glynn, *J. Mar. Res.* **35**, 567 (1977).
7. P. W. Glynn, M. W. Colgan, *Am. Zool.* **32**, 707 (1992).
8. C. M. Eakin, *Coral Reefs* **15**, 109 (1996).
9. P. W. Glynn, I. G. Macintyre, *Proc. 3rd Int. Coral Reef Symp.*, 251 (1977).
10. Materials and methods are available as supplementary materials on *Science Online*.
11. I. Martínez, D. Rincon, Y. Yokoyama, T. Barrows, Foraminifera and coccolithophorid assemblage changes in the Panama Basin during the last deglaciation: Response to sea-surface productivity induced by a transient climate change. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **234**, 114 (2006). [doi:10.1016/j.palaeo.2005.10.022](https://doi.org/10.1016/j.palaeo.2005.10.022)
12. J. Cortés, I. G. Macintyre, P. W. Glynn, Holocene growth history of an eastern Pacific fringing reef, Punta Islotes, Costa Rica. *Coral Reefs* **13**, 65 (1994). [doi:10.1007/BF00300763](https://doi.org/10.1007/BF00300763)
13. C. T. Perry, S. G. Smithers, Evidence for the episodic “turn on” and “turn off” of turbid-zone coral reefs during the late Holocene sea-level highstand. *Geology* **38**, 119 (2010). [doi:10.1130/G30444.1](https://doi.org/10.1130/G30444.1)
14. M. Lybolt *et al.*, Instability in a marginal coral reef: The shift from natural variability to a human-dominated seascape. *Front. Ecol. Environ.* **9**, 154 (2011). [doi:10.1890/090176](https://doi.org/10.1890/090176)
15. N. Hamanaka *et al.*, Disturbances with hiatuses in high-latitude coral reef growth during the Holocene: Correlation with millennial-scale global climate change. *Global Planet. Change* **80**, 21 (2012). [doi:10.1016/j.gloplacha.2011.10.004](https://doi.org/10.1016/j.gloplacha.2011.10.004)
16. G. H. Haug, K. A. Hughen, D. M. Sigman, L. C. Peterson, U. Röhl, Southward migration of the intertropical convergence zone through the Holocene. *Science* **293**, 1304 (2001). [doi:10.1126/science.1059725](https://doi.org/10.1126/science.1059725) [Medline](#)
17. M. A. Riedinger, M. Steinitz-Kannan, W. M. Last, M. Brenner, *J. Paleolimnol.* **27**, 1 (2002). [doi:10.1023/A:1013514408468](https://doi.org/10.1023/A:1013514408468)

18. B. Rein, How do the 1982/83 and 1997/98 El Niños rank in a geological record from Peru? *Quat. Int.* **161**, 56 (2007). [doi:10.1016/j.quaint.2006.10.023](https://doi.org/10.1016/j.quaint.2006.10.023)
19. J. L. Conroy, J. T. Overpeck, J. E. Cole, T. M. Shanahan, M. Steinitz-Kannan, Holocene changes in eastern tropical Pacific climate inferred from a Galápagos lake sediment record. *Quat. Sci. Rev.* **27**, 1166 (2008). [doi:10.1016/j.quascirev.2008.02.015](https://doi.org/10.1016/j.quascirev.2008.02.015)
20. T. H. Donders, F. Wagner-Cremer, H. Visscher, Integration of proxy data and model scenarios for the mid-Holocene onset of modern ENSO variability. *Quat. Sci. Rev.* **27**, 571 (2008). [doi:10.1016/j.quascirev.2007.11.010](https://doi.org/10.1016/j.quascirev.2007.11.010)
21. T. Corrège *et al.*, Evidence for stronger El Niño-Southern Oscillation (ENSO) events in a Mid-Holocene massive coral. *Paleoceanography* **15**, 465 (2000). [doi:10.1029/1999PA000409](https://doi.org/10.1029/1999PA000409)
22. M. K. Gagan, E. J. Hendy, S. G. Haberle, W. S. Hantoro, Post-glacial evolution of the Indo-Pacific Warm Pool and El Niño-Southern oscillation. *Quat. Int.* **118-119**, 127 (2004). [doi:10.1016/S1040-6182\(03\)00134-4](https://doi.org/10.1016/S1040-6182(03)00134-4)
23. M. S. Lachniet *et al.*, A 1500-year El Niño/Southern Oscillation and rainfall history for the Isthmus of Panama from speleothem calcite. *J. Geophys. Res.* **109**, D20117 (2004). [doi:10.1029/2004JD004694](https://doi.org/10.1029/2004JD004694)
24. J. A. Kleypas, Modeled estimates of global reef habitat and carbonate production since the Last Glacial Maximum. *Paleoceanography* **12**, 533 (1997). [doi:10.1029/97PA01134](https://doi.org/10.1029/97PA01134)
25. M. Collins *et al.*, The impact of global warming on the tropical Pacific Ocean and El Niño. *Nat. Geosci.* **3**, 391 (2010). [doi:10.1038/ngeo868](https://doi.org/10.1038/ngeo868)
26. C. M. Moy, G. O. Seltzer, D. T. Rodbell, D. M. Anderson, Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch. *Nature* **420**, 162 (2002). [doi:10.1038/nature01194](https://doi.org/10.1038/nature01194) [Medline](#)
27. H. Yan *et al.*, A record of the Southern Oscillation Index for the past 2,000 years from precipitation proxies. *Nat. Geosci.* **4**, 611 (2011). [doi:10.1038/ngeo1231](https://doi.org/10.1038/ngeo1231)
28. R. Wood, *Reef Evolution* (Oxford Univ. Press, New York, 1999).
29. R. W. Buddemeier, D. Hopley, *Proc. 6th Int. Coral Reef Symp.*, 253 (1988).
30. J. R. Curray, F. J. Emmel, P. J. S. Crampton, *Lagunas Costeras, Un Simposio, Memorias del Simposio Internacional sobre Lagunas Costeras*, A. A. Castañares, F. B. Phleger, Eds. (Universidad Nacional Autónoma de México–United Nations Educational, Scientific, and Cultural Organization, México D.F., 1969), pp. 63–100.
31. M. A. Toscano, I. G. Macintyre, Corrected western Atlantic sea-level curve for the last 11,000 years based on calibrated ¹⁴C dates from *Acropora palmata* framework and intertidal mangrove peat. *Coral Reefs* **22**, 257 (2003). [doi:10.1007/s00338-003-0315-4](https://doi.org/10.1007/s00338-003-0315-4)
32. U.S. Geological Survey, *U.S. Geol. Surv. Open-File Rep.* 98-779 (1998).
33. J. L. Sonnenholzner, L. B. Ladah, K. D. Lafferty, Cascading effects of fishing on Galapagos rocky reef communities: Reanalysis using corrected data. *Mar. Ecol. Prog. Ser.* **375**, 209 (2009). [doi:10.3354/meps07890](https://doi.org/10.3354/meps07890)

34. A. C. Baker, P. W. Glynn, B. Riegl, Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar. Coast. Shelf Sci.* **80**, 435 (2008). [doi:10.1016/j.ecss.2008.09.003](https://doi.org/10.1016/j.ecss.2008.09.003)
35. D. M. Thompson, R. van Woesik, Corals escape bleaching in regions that recently and historically experienced frequent thermal stress. *Proc. Biol. Sci.* **276**, 2893 (2009). [doi:10.1098/rspb.2009.0591](https://doi.org/10.1098/rspb.2009.0591) [Medline](#)
36. M. R. Dardeau, R. B. Aronson, W. F. Precht, I. G. Macintyre, *20th Symp. Am. Acad. Underwater Sci.*, 6 (2000).
37. R. B. Aronson, I. G. Macintyre, W. F. Precht, T. J. T. Murdoch, C. M. Wapnick, The expanding scale of species turnover events on coral reefs in Belize. *Ecol. Monogr.* **72**, 233 (2002). [doi:10.1890/0012-9615\(2002\)072\[0233:TESOST\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2002)072[0233:TESOST]2.0.CO;2)
38. M. Stuiver, H. A. Polach, *Radiocarbon* **19**, 355 (1977).
39. P. J. Reimer, R. W. Reimer, *Radiocarbon* **43**, 461 (2001).
40. P. J. Reimer *et al.*, *Radiocarbon* **51**, 1111 (2009).
41. B. L. Ingram, Differences in radiocarbon age between shell and charcoal from a holocene shellmound in northern California. *Quat. Res.* **49**, 102 (1998). [doi:10.1006/qres.1997.1944](https://doi.org/10.1006/qres.1997.1944)
42. M. Fontugne, M. Carré, I. Bentaleb, M. Julien, D. Lavallée, *Radiocarbon* **46**, 531 (2004).
43. A. M. M. Soares, J. M. A. Dias, *Radiocarbon* **48**, 45 (2006).
44. E. R. M. Druffel *et al.*, Low reservoir ages for the surface ocean from mid-Holocene Florida corals. *Paleoceanography* **23**, PA2209 (2008). [doi:10.1029/2007PA001527](https://doi.org/10.1029/2007PA001527)
45. E. Bard, B. Hamelin, R. G. Fairbanks, A. Zindler, Calibration of the ¹⁴C timescale over the past 30,000 years using mass spectrometric U-Th ages from Barbados corals. *Nature* **345**, 405 (1990). [doi:10.1038/345405a0](https://doi.org/10.1038/345405a0)
46. E. Bard, M. Arnold, R. G. Fairbanks, B. Hamelin, *Radiocarbon* **35**, 191 (1993).
47. M. Stuiver, P. J. Reimer, E. Bard, J. W. Spurk, *Radiocarbon* **40**, 1041 (1998).
48. L. K. Zaunbrecher, thesis, Georgia Institute of Technology, Atlanta, GA (2009).
49. W. J. Conover, R. L. Iman, *Am. Stat.* **35**, 124 (1981).
50. I. G. Macintyre, P. W. Glynn, *Am. Assoc. Pet. Geol. Bull.* **60**, 1054 (1976).
51. R. B. Aronson, I. G. Macintyre, C. M. Wapnick, M. W. O'Neill, Phase shifts, alternative states, and the unprecedented convergence of two reef systems. *Ecology* **85**, 1876 (2004). [doi:10.1890/03-0108](https://doi.org/10.1890/03-0108)
52. M. Stuiver, P. J. Reimer, *Radiocarbon* **35**, 215 (1993).
53. M. Stuiver, P. J. Reimer, R. W. Reimer, <http://calib.qub.ac.uk/calib> (2005).
54. C. M. Wapnick, W. F. Precht, R. B. Aronson, Millennial-scale dynamics of staghorn coral in Discovery Bay, Jamaica. *Ecol. Lett.* **7**, 354 (2004). [doi:10.1111/j.1461-0248.2004.00586.x](https://doi.org/10.1111/j.1461-0248.2004.00586.x)

55. L. F. Montaggioni, History of Indo-Pacific coral reef systems since the last glaciation: Development patterns and controlling factors. *Earth Sci. Rev.* **71**, 1 (2005). [doi:10.1016/j.earscirev.2005.01.002](https://doi.org/10.1016/j.earscirev.2005.01.002)
56. J. Cortés, *Rev. Biol. Trop.* **41**, 19 (1993).
57. I. G. Macintyre, R. B. Burke, R. Stuckenrath, Thickest recorded Holocene reef section, Isla Pérez core hole, Alacran Reef, Mexico. *Geology* **5**, 749 (1977). [doi:10.1130/0091-7613\(1977\)5<749:TRHRSI>2.0.CO;2](https://doi.org/10.1130/0091-7613(1977)5<749:TRHRSI>2.0.CO;2)